

中国萱草属(百合科)的数量细胞分类研究*

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NUMERICAL CYTOTAXONOMIC STUDIES OF *HEMEROCALLIS* (LILIACEAE) FROM CHINA

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Abstract Comparative studies of karyotypes in *Hemerocallis* from China have been carried out using numerical techniques. Taxa studied are as follows: *Hemerocallis citrina*, *H. dumortieri*, *H. esculenta*, *H. forrestii*, di- and triploid *H. fulva*, *H. lilioasphodelus*, *H. middendorffii*, *H. minor*, *H. multiflora* and *H. plicata*. The results show that variation in speciation has taken place at chromosomal level, and that karyotype variations have largely paralleled the morphological ones. Taxonomic proposals are given to treat *H. citrina* and *H. minor* as subspecies of *H. lilioasphodelus*, and *H. esculenta* as a variety of *H. dumortieri*. The results are not in favour of considering *H. middendorffii* as a variety of *H. dumortieri*, and *H. multiflora* closely related to *H. plicata*.

Key words *Hemerocallis*; Karyotype; Numerical cytotaxonomy; China

Hemerocallis occurs mainly in China, with some species extending to Mongolia, Siberia, Korea and Japan. For a long time, taxonomy of the genus was a difficult task due to morphological continuity among the taxa. It has tentatively been estimated to have 14 (Chen, 1980) or 21 (Hu, 1968) species. The important taxonomic problems of the genus remaining unsolved at this time are: (a) if *H. lilioasphodelus*, *H. citrina* and *H. minor* are different species or different varieties of the same species; (b) if *H. dumortieri*, *H. esculenta* and *H. middendorffii* are different species or different varieties of the same species; and (c) if *H. multiflora*, a Chinese endemic species, is closely related to another Chinese endemic species, *H. plicata* or not (Xiong *et al.*, 1997b, 1996; Chen, 1980; Hu, 1968; Matsuoka & Hotta, 1966; Ohwi, 1965; Kitamura, 1964).

Investigations on chromosome number and morphology of almost all species in the genus were carried out. Only one basic number, $x = 11$, has been found. With exception of *H. aurantiaca* and *H. fulva* in which triploid ($2n = 33$) has been observed, the species are all diploid ($2n = 22$) (Jin, 1985; Zadoo *et al.*, 1976; Matsuoka, 1971; Chandler, 1940; Dark, 1932; Stout, 1932). Descriptions of chromosome morphology in the literature are not always

* This research was supported by the National Natural Science Foundation of China, Project 39670050.
1997-07-02 收稿, 1998-01-12 收最后修改稿。

detailed or comparable due to different features and standards used (Xiong *et al.*, 1998, 1997a; Hong & Sauer, 1990; Noguchi, 1986; Jin, 1985; Vij *et al.*, 1978; Zadoo *et al.*, 1976; Kawano, 1961; Sato, 1942). Based on the observation of karyotypes of 12 species and comparison with previous reports, Jin (1985) concluded that the genus was more or less uniform for gross chromosome structure, and speciation seemed to have taken place at gene level. In other words, the karyotype data reported appeared to be of little taxonomic significance.

In a comparative study of karyotypes among *H. citrina* and *H. fulva* complex using a numerical method, cluster analysis, however, it was found that karyotype divergence is comparable well with the accepted classification of these taxa (Xiong & Chen, 1992). The fact suggests that karyotype data be of taxonomic significance in the genus. The present paper is an attempt to solve the taxonomic problems mentioned above by numerical analysis of karyotypes of the genus from China.

1 Materials and methods

Materials used are listed in Table 1. The voucher specimens were identified according to Chen (1980). Most species were tested with two or more samples collected from different locations.

Plants were transplanted from the wild into a greenhouse and grown in porcelain pots. Root-tips were excised from adventitious roots of underground stems, pretreated at room temperature in 0.05% aqueous solution of colchicine for 3 h, fixed in Carnoy's fixative (glacial acetic acid : absolute ethanol = 1:3) overnight at 6 °C, then transferred into 70% ethanol and stored in a refrigerator. Prior to staining, the stored root-tips were hydrolysed for 1 min in 1 mol/L HCl at 60 °C. Then they were stained in Carbol fuchsin for 30 min and squashed. Slides were frozen in liquid N₂ for removing of cover slips, dehydrated and mounted in Canada balsam. Photographs were taken on a Leitz photomicroscope at a magnification of $\times 1250$.

Chromosome arm length was measured on photographs. The relative length (= long arm + short arm) and arm ratio (= long arm / short arm) of a chromosome were calculated based on the measurements. Centromere position was defined following Levan *et al.* (1964).

Homologous chromosomes in a complement were paired according to their lengths and arm ratios. In order to pair the homologues as accurately as possible, the 11 pairs were divided into 4 groups (Table 2), each characterized with its own features. The first group included two pairs which were the longest in the complement. Of them, the one with smaller arm ratio was labeled No. 1, the other No. 2. The second group included three pairs which were characterized by an arm ratio smaller than the remaining 6, and were distinguished from one another by length, the longest as No. 3, the second longest No. 4, and the other No. 5 which was also the shortest in the complement. The third group included another three pairs whose arm ratios were smaller than the last 3. They were not always distinguishable from one another by length. Therefore they were arranged based on arm ratio: No. 6 < No. 7 < No. 8 in arm ratio. The fourth group included the 3 pairs whose arm ratios were larger than any of the others in the complement. Among them, that with a terminal centromere was labeled as No. 11, and No. 9 was longer than No. 10.

Each species was treated as an operational taxonomic unit (OTU), with *H. fulva* as only exception, of which the diploid and triploid were treated as different OTUs. For each

OTU, there were 22 karyotypical characters, 11 relative lengths and 11 arm ratios (Table 3). Different samples of the same OTU (Table 1) were pooled and means of the 22 characters were calculated respectively. Each character was standardized by dividing with the corresponding maximum. Cluster analysis, a classic numerical taxonomic method, was applied to estimate karyotypical phenetic relationships among taxa. Euclidean distances were calculated to determine dissimilarity between OTUs based on the standardized data matrix. Unweighted pair-group method using arithmetic averages (UPGMA) was used as fusion strategy (Sneath & Sokal, 1973).

Table 1 *Hemerocallis* species studied, and their vouchers

Species	Locality	Altitude (m)	Cells Observed	Voucher(PE)
<i>H. citrina</i> Baroni	She Xian, Hebei	500	5	Xiong 90015
	Qidong, Hunan	200	12	Xiong 91021, 91023, 91024
	Maoshan, Jiansu	180	5	Xiong 91044
<i>H. dumortieri</i> Morren	Long Xian, Shaanxi	2300	16	Xiong 910531, 910532, 910533
<i>H. esculenta</i> Koidzumi	Wuan, Hebei	1200	18	Xiong 90011, 90012, 90013, 90014
	Shennongjia, Hubei	2100	5	Xiong 92068
<i>H. forrestii</i> Diels	Lijiang, Yunnan	3200	17	Xiong 91037, 91038, 91039
<i>H. fulva</i> (L.) L. (diploid)	Mt. Jigong, Henan	700	8	Xiong 91047, 91050
	Wufeng, Hubei	1020	4	Xiong 90010
	Shaoguan, Guangdong	not recorded	5	Xiong 91017
	Mt. Wuyi, Fujian	not recorded	5	Xiong 91071
<i>H. fulva</i> (L.) L. (triploid)	Shennongjia, Hubei	1350	4	Xiong 91028
	Qidong, Hunan	500	5	Xiong 91025
	Shaoguan, Guangdong	not recorded	8	Xiong 91018, 91019
	Dali, Yunnan	2500	8	Xiong 91036, 91041
<i>H. lilioasphodelus</i> L. emend Hylander	Mentougou, Beijing	800	5	Xiong 90008
	Mt. Lao, Shandong	200	10	Xiong 91064, 91065
	Baihe, Jilin	710	5	Xiong 91057
<i>H. middendorffii</i> Trautvetter & Meyer	Baihe, Jilin	760	10	Xiong 91056, 91058
	Tonghua, Jilin	500	5	Xiong 91063
<i>H. minor</i> Miller	Baoqing, Heilongjiang	300	10	Xiong 92069
	Mt. Baihua, Beijing	2000	8	Xiong 90007
<i>H. multiflora</i> Stout	Mt. Jigong, Henan	780	15	Xiong 910481, 910482
<i>H. plicata</i> Stapf	Kunming, Yunnan	2300	11	Xiong 91029, 91030
	Dali, Yunnan	2300	8	Xiong 91042

Table 2 Centromere position types of chromosome complements of 11 taxa of *Hemerocallis* from China

Species(2n)	Chromosome No.										
	1	2	3	4	5	6	7	8	9	10	11
	Group 1		Group 2			Group 3			Group 4		
<i>H. citrina</i> (22)	m	m*	m	m	m	m	sm	sm	st*	st*	T*
<i>H. dumortieri</i> (22)	m	m	m	m	m	m	sm	sm	sm	sm*	T*
<i>H. esculenta</i> (22)	m	m	m	m	m	m	sm	sm	sm*	sm*	T*
<i>H. forrestii</i> (22)	m	m	m	m	m	sm	sm	sm	sm	sm	T*
<i>H. fulva</i> (22)	m	m	m	m	m	m	sm	sm	sm*	st*	T*
<i>H. fulva</i> (33)	m	m	m	m	m	m	sm*	sm	sm*	st*	T*
<i>H. lilioasphodelus</i> (22)	m	m	m	m	m	m	sm	sm	st*	st*	T*
<i>H. middendorffii</i> (22)	m	m	m	m	m	sm	sm	sm	st*	st*	T*
<i>H. minor</i> (22)	m	m	m	m	m	m	sm	sm	st*	st*	T*
<i>H. multiflora</i> (22)	m	m	m	m	m	m	sm	sm	sm	sm	T*
<i>H. plicata</i> (22)	m	m	m	m	m	m	sm	sm	sm	sm	T*

Centromere position types are determined following Levan *et al.* (1964).

"*" indicates terminal point microsatellite on the short arm of a chromosome.

Xiong *et al.* (1992) proposed a numerical method for estimating karyotypical asymmetry of a complement in terms of arm ratio and length, by which karyotypical asymmetry differences among taxa could be revealed without need of determining their homologous chromosomes in advance. This method was applied here also. Two coefficients Dc and Dt were to be determined for each taxon(OTU) based on arm ratio and length respectively. In a simplified form, the coefficients are expressed here as $Dc = \sum_{i=1}^x (1 - \frac{1}{r_i})$ and $Dt = \frac{1}{4} \sum_{i=1}^x |l_i - \frac{100}{x}|$, where x = basic number, r = arm ratio, and l = relative length(%).

2 Results

Karyograms of 11 taxa are shown in Fig. 1. Centromere position types of the taxa are listed in Table 2. Chromosomes of all the taxa in group 1(No. 1 and No. 2) and group 2(No. 3, No. 4 and No. 5) are m type, No. 7 and No. 8 sm type and No. 11 T type. The other 3 chromosomes(No. 6, No. 9 and No. 10) are m, sm or st type, depending on taxa. Compared on the centromere position type of a whole complement, there is no difference between *H. lilioasphodelus*, *H. citrina*, *H. minor* and *H. multiflora*. This is also true between di- and triploid *H. fulva*, and between *H. dumortieri*, *H. esculenta* and *H. plicata*. However, as far as microsatellite number is concerned, *H. multiflora* is different from the other three, and *H. plicata* from the other two species in their groups.

Result of the cluster analysis is shown as a dendrogram in Fig. 2. It is divided into three clusters at a higher fusion level. The first cluster includes *H. dumortieri*, *H. esculenta*, *H. plicata* and *H. forrestii*, and the former two species fuse at a very low level of 0.0700. The second cluster only includes di- and triploid *H. fulva* and it further fuses with the third cluster at 0.4860 level. In the third cluster, *H. citrina* and *H. minor* fuse with *H. lilioasphodelus* also at relatively low levels. Note that in the dendrogram *H. middendorffii* is far removed from *H. dumortieri* and *H. esculenta*, which were considered to belong to the same species(Ohwi, 1965; Kitamura, 1964).

Table 3 Karyotype characters of 11 taxa of *Hemerocallis* from China*

Character**	Ci	Du	Es	Fo	F2	F3	Li	Md	Mi	Mu	Pl
1	6.83	6.60	6.64	6.82	6.56	6.57	6.68	6.69	6.63	6.60	6.86
2	6.39	6.14	6.17	6.28	6.52	6.52	6.37	6.24	6.51	6.61	6.19
3	4.76	4.97	4.98	4.89	4.97	4.98	4.81	4.88	4.71	4.82	4.92
4	4.43	4.44	4.42	4.17	4.44	4.24	4.33	4.46	4.32	4.41	4.12
5	3.15	3.30	3.26	3.23	3.17	3.23	3.20	3.22	3.34	3.11	3.29
6	4.44	4.49	4.54	4.55	4.16	4.12	4.50	4.38	4.44	4.14	4.37
7	4.44	4.49	4.52	4.19	4.41	4.55	4.53	4.45	4.46	4.61	4.32
8	8.31	4.28	4.18	4.52	4.57	4.48	4.33	4.42	4.32	4.43	4.38
9	4.04	4.17	4.13	4.14	4.10	4.14	3.98	4.04	4.03	4.09	4.28
10	3.56	3.63	3.57	3.68	3.55	3.60	3.56	3.68	3.69	3.51	3.58
11	3.66	3.54	3.59	3.53	3.54	3.57	3.64	3.54	3.64	3.59	3.69
12	1.37	1.29	1.31	1.25	1.15	1.15	1.40	1.35	1.50	1.38	1.23
13	1.60	1.64	1.61	1.79	1.27	1.29	1.59	1.61	1.61	1.64	1.66
14	1.38	1.24	1.26	1.23	1.10	1.08	1.37	1.30	1.34	1.48	1.09
15	1.48	1.44	1.45	1.25	1.32	1.31	1.42	1.50	1.45	1.47	1.32
16	1.48	1.13	1.16	1.03	1.26	1.25	1.52	1.28	1.48	1.56	1.14
17	1.61	1.66	1.69	1.88	1.47	1.52	1.64	1.81	1.65	1.58	1.66
18	2.06	1.92	1.86	2.30	1.76	1.88	2.14	2.20	2.09	2.20	1.92
19	2.44	2.29	2.32	2.46	2.10	2.18	2.43	2.44	2.38	2.48	2.12
20	3.73	2.78	2.69	2.86	2.93	2.73	3.39	3.41	3.58	4.30	2.47
21	4.74	2.43	2.26	2.97	4.89	4.41	4.86	4.29	4.81	5.10	2.66
22	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞

* For names of the species see Fig. 1.

** Characters 1~11 are relative lengths respectively for chromosomes No. 1~11, 12~22 arm ratios respectively for chromosomes No. 1~11

There are ten fusion steps in total from lower to higher dissimilarity level in the construction of the dendrogram (Fig. 2). At the fourth step of 0.1419 level fuse the intraspecific taxa di- and triploid *H. fulva*. At the next step of 0.2200 level, *H. plicata* fuses with *H. dumortieri* and *H. esculenta*. *H. plicata* is distinguishable from the latter two as a different species without any question. Therefore, it would be reasonable to consider the interval of dissimilarity between step 4 and step 5 as a transition from intra- to interspecies.

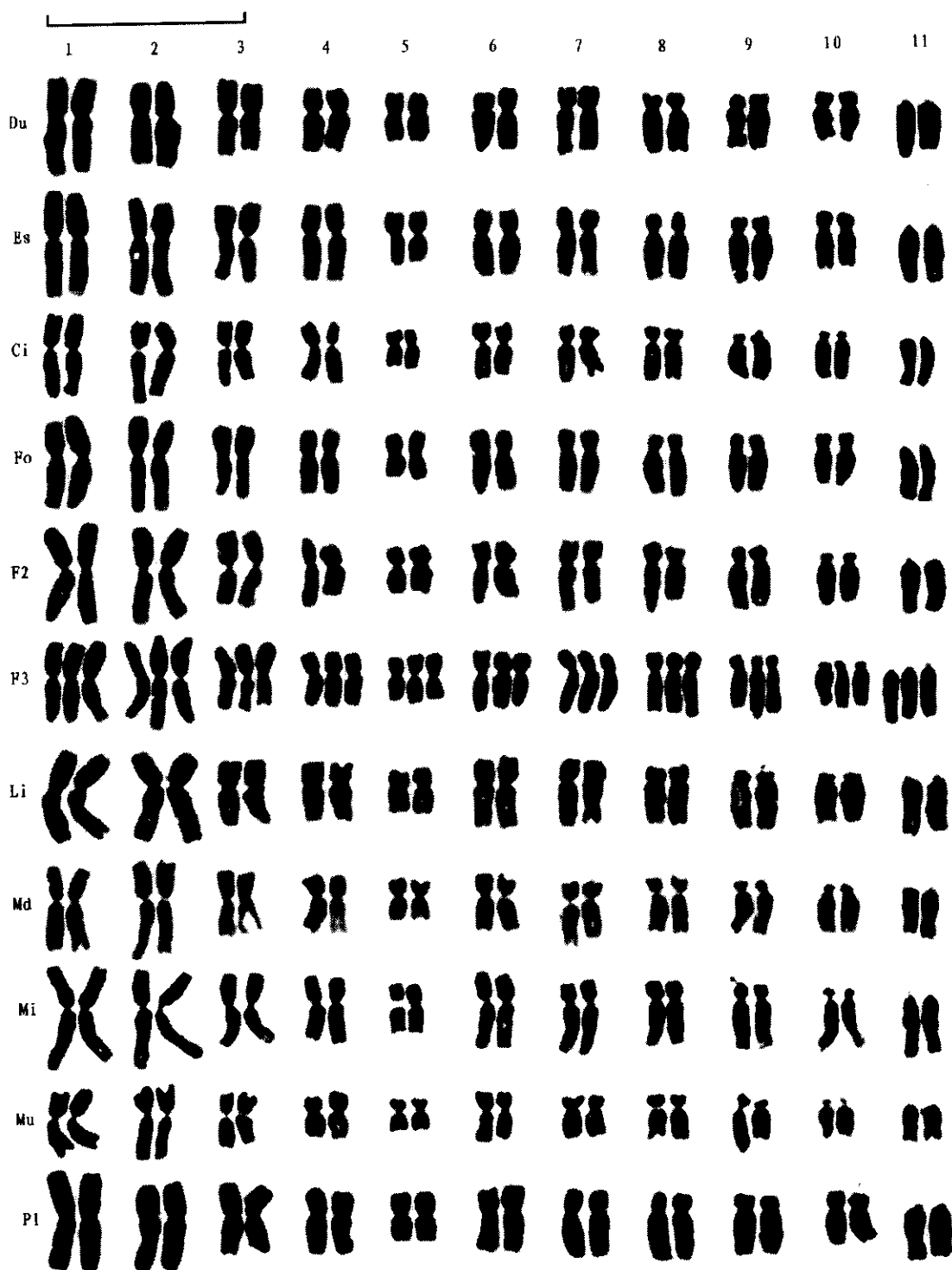


Fig. 1 Carbol fuchsin-stained somatic chromosomes of *Hemerocallis*. Du: *H. dumortieri*; Es: *H. esculenta*; Ci: *H. citrina*; Fo: *H. forrestii*; F2: diploid *H. fulva*; F3: triploid *H. fulva*; Li: *H. lilioasphodelus*; Md: *H. middendorffii*; Mi: *H. minor*; Mu: *H. multiflora*; Pl: *H. plicata*. Homologous chromosomes are paired. Pairs are arranged in the same sequence as in Table 2. Bar = 10 μ m.

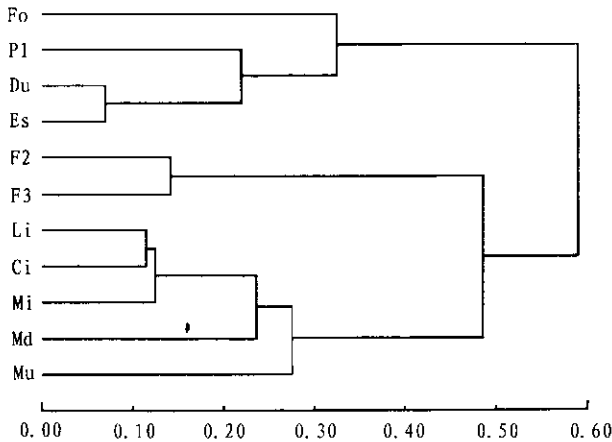


Fig. 2 Dendrogram of cluster analysis of *Hemerocallis* karyotypes based on 11 chromosome lengths and 11 arm ratios using Euclidean distance as dissimilarity coefficient and UPGMA as fusion strategy (Sneath & Sokal, 1973). For names of the species see Fig. 1.

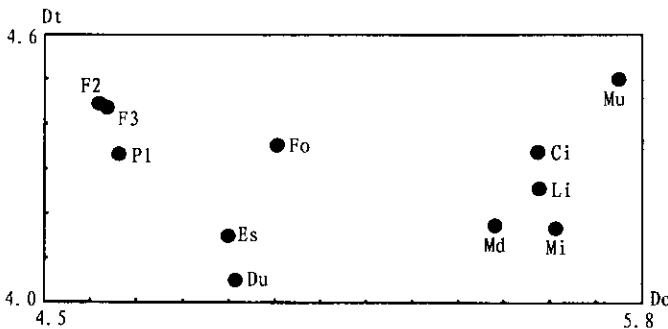


Fig. 3 Plot of karyotype asymmetry analysis of *Hemerocallis* based on 11 chromosome lengths and 11 arm ratios using the method by Xiong *et al.* (1992). For names of the species see Fig. 1.

The result of karyotype asymmetry analysis is shown in Fig. 3. In the plot, Dc and Dt represent asymmetry variation in arm ratio and length respectively. On dimension Dc, *H. multiflora* has the highest karyotype asymmetry. It is followed by *H. lilioasphodelus*, *H. citrina*, *H. minor* as well as *H. middendorffii*. At lower asymmetry levels are *H. forrestii*, *H. dumortieri* and *H. esculenta*. *H. fulva* has the lowest asymmetry, and that of *H. plicata* is only a little higher than *H. fulva*. On dimension Dt, *H. multiflora* also has the highest asymmetry, followed by *H. fulva*. Asymmetry of *H. dumortieri* is the lowest. The asymmetry of the other taxa vary between the two ends. It should be pointed out that the variation of Dt value among taxa is not as distinctive as that of Dc (Fig. 3). Also, a principal components analysis of the karyotypes

showed that average loading of a length character on the first three components was only 75% of that of an arm ratio one (data not shown). These might imply that karyotype asymmetry variations in the *Hemerocallis* genome were chiefly attributed to centromere position change.

3 Discussion

The dendrogram (Fig. 2) and the plot (Fig. 3) are similar to each other in basic structure. Taxa fused at higher levels of similarity in the dendrogram (i. e. Du and Es, F2 and F3, and Li, Ci and Mi) also group closely in the plot. It suggests that these taxa be closely related to each other in karyotypical phenetic relationship, and hence they are very likely to be of intraspecific taxa.

H. lilioasphodelus is the type species of the genus. *H. minor* and *H. citrina* were published in 1768 and 1897 respectively. Matsuoka & Hotta (1966) treated *H. minor* as one of the varieties of *H. lilioasphodelus*. Recently, based on a comprehensive taxonomic

study of the nocturnal flowering group in the genus, Xiong *et al.* (1996) proposed that *H. minor* and *H. citrina* should be treated as subspecies of *H. lilioasphodelus*. As a matter of fact, almost all morphological diagnostic characters in the literature were continuous among the three taxa (Xiong *et al.*, 1996). In China, they appear to have somewhat different distributions. However, in their overlapping distribution areas, so much variation in plants was observed that it was not possible to draw a clear distinction between them. The high karyotypical similarity among them (Fig. 2 and Fig. 3) is consistent with their high morphological similarity (Xiong *et al.*, 1997b, 1996).

Botanists have long been puzzled by the taxonomic uncertainty of *H. esculenta*. Koidzumi considered it close to *H. thunbergii* (see Hu, 1968). Stout (1935) mentioned it as a taxon included in *H. fulva*. Later, it was treated as a variety of either *H. dumortieri* (Kitamura, 1964) or *H. middendorffii* (Ohwi, 1965). In China, Chen (1980) conserved it as a species, though he believed it to be close to *H. dumortieri* and *H. middendorffii*. The high karyotypical similarity between *H. dumortieri* and *H. esculenta* (Fig. 2 and Fig. 3) clearly indicates a close relationship between them, and supports Kitamura's treatment (1964).

Considerable variation in wild plants has sometimes confused *H. dumortieri* and *H. middendorffii* in Japan (Stout, 1935). Kitamura (1964) treated *H. middendorffii* as another variety of *H. dumortieri*. However, distinguishing *H. middendorffii* from *H. dumortieri* is usually not difficult because of its unique inflorescence which is wholly clasped by large, overlapping and shell-like bracts (Chen, 1980; Hu, 1968). Furthermore, their distribution areas are different in China with small overlapping in Liaoning Province in northeastern China (Chen, 1980). *H. middendorffii* never ranges down to 40° N, whereas *H. dumortieri* can be found in latitudes down to 35° N. Karyotype dissimilarity between them is considerable (Fig. 2) and karyotype asymmetry of *H. middendorffii* is much larger than *H. dumortieri* (Fig. 3). The present results, together with morphology and distribution data, support the treatment of keeping *H. middendorffii* as a species rather than a variety of *H. dumortieri*.

There are four Chinese-endemic species in the genus, i. e. *H. nana*, *H. plicata*, *H. forrestii* and *H. multiflora*. The first three species occur in southwestern China, while *H. multiflora* has been found only in Henan Province in central China. Chinese botanists all agree that *H. nana* is related to *H. forrestii* (Xiong *et al.*, 1997b; Chen, 1980; Hu, 1968). However, they differ in their views on relationships among the last three species. Hu (1968) considered that the true relationship of *H. plicata* was with *H. multiflora*. However, Chen (1980) believed that *H. plicata* was closely related to *H. forrestii*. Recently we observed pollen morphology of all the species in the genus from China and found that *H. plicata*, *H. forrestii* and *H. nana* have verrucate pollen, while the others, including *H. multiflora*, have reticulate pollen (Xiong *et al.*, 1997c). In the present study, the results show that karyotype differences between *H. plicata* and *H. forrestii* are much smaller than those between *H. plicata* and *H. multiflora* (Fig. 2 and Fig. 3). Therefore, evidence from phytogeography, pollen morphology and karyotype has favoured the suggestion that *H. plicata* is closely related to *H. forrestii* instead of *H. multiflora*.

A numerical taxonomic study of the genus based on 30 morphological characters was carried out recently (Xiong *et al.*, 1997b). Three clusters were distinguished in that dendrogram: Du, Md, Pl, Fo, Na; F2, F3; Li, Mi, Ci, Mu. Obviously, the karyotype dendro-

gram(Fig. 2) is similar to the gross morphology one, except in *H. middendorffii* which is included in non-corresponding clusters in the two dendrograms. This parallel between karyotypical and morphological variation suggests that variation in speciation in the genus has taken place at the chromosomal level although chromosome morphology is more or less uniform. As for the close karyotypical similarity of *H. middendorffii* with the species from which it differs in gross morphology, the mechanisms are uncertain. Heterochromatin or satellite DNA variation might have been concerned. Therefore, further studies using more powerful molecular cytology techniques are needed to solve this problem.

In conclusion, the results from numerical analysis of karyotype clearly indicate that variation in speciation has taken place at the chromosomal level in *Hemerocallis*, and karyotype data are valuable in solving phylogenetic relationships in the genus. The results support proposals to treat *H. citrina* and *H. minor* as subspecies of *H. lilioasphodelus*, and *H. esculenta* as a variety of *H. dumortieri*. On the other hand, they do not support suggestions that *H. middendorffii* be a variety of *H. dumortieri*, and *H. multiflora* closely related to *H. plicata*. The results also reveal that karyotypic variation matches gross morphological variation, although in some cases convergent evolution in karyotype might have occurred.

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摘要 用数量分类技术比较研究了国产萱草属植物的核型。所研究的分类群是: *Hemerocallis citrina*, *H. dumortieri*, *H. esculenta*, *H. forrestii*, 二倍体和三倍体 *H. fulva*, *H. lilioasphodelus*, *H. middendorffii*, *H. minor*, *H. multiflora*, *H. plicata*。结果表明,物种形成已发生在染色体水平,染色体变异与形态变异基本一致。结果支持将 *H. citrina* 和 *H. minor* 作为 *H. lilioasphodelus* 的亚种, *H. esculenta* 作为 *H. dumortieri* 的变种。结果不支持将 *H. middendorffii* 作为 *H. dumortieri* 的变种,也没有发现 *H. multiflora* 与 *H. plicata* 密切相关的证据。

关键词 萱草属; 核型; 数量细胞分类; 中国